ON THE RADULÆ OF THE BRITISH HELICIDS. (Part II.)

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[The terminology proposed in this paper has been revised in accordance with suggestions made by the President and other members of the Society.]

It is necessary to add to the number of technical terms used for describing the parts of the radula, because the microscopic methods and apparatus now at our disposal give a much more perfect view of the structures in question. It will further be desirable to define the terms now employed.

The *radula* is an oblongate membrane disposed with its long sides roughly parallel to the sides of the snail's body. It is, in the forms now under consideration, enclosed in a muscular organ called the *odontophore*, which is the atrium of the digestive system. In its front portion the odontophore also carries the *maxilla* (= jaw; the 'machoire' of French authors), which seizes the food, and perhaps also assists in holding it in position while it is being rasped into small pieces by the radula. The radula is provided with regularly disposed rows of *unci* or hooks, the front and upper portions of which have long been called teeth. It is not yet certain whether these unci bear any relation to the parasphenoidal teeth of such forms as *Batrachoseps* among the vertebrates.

The *unci* are arranged with their free cutting points directed towards the œsophagus of the animal. These points are called *cones*. Where more than one cone occurs on each uncus, the terms *mesocone*, *ectocone*, and *endocone* will naturally be used. In some cases it may be advantageous to draw a distinction between endocone plus mesocone, and bifid mesocone or bifid endocone; but the truth of such determinations can only be settled by sections showing the groups of cells in the *radular sac* (the infolded inner end of the radula) from which the unci originate.

Rücker[1] has shown the mode of development of the unci in *Helix pomatia*. The mechanical difficulties in sectioning such material are considerable, but it seems certain that each uncus in each longitudinal row is a cast of the same matricial cell or group of cells, situated on the lower wall of the radular sac. (This accounts for the regularity with which any asymmetry in development is repeated throughout the length of the radula.) A question which seems to call for settlement is, how is this cast produced? Is it (*a*) a membrane detached from the top of the matricial cell or cells? (Microscopic examination of unsectioned, but stained, radulæ favour this interpretation.) Or is it (*b*) a chitinous structure actually secreted by all the cells which surround it in the radular sac, and only owing its definite form to the impress of these strangely enlarged and persistent matricial cells?

[1] Bericht d. Oberhass. Ges. Natur. u. Heilkunde, 1883, vol. xxii.

It should be noted that the unci do not attain their full development till they reach the middle of the radula; up to that point they continue to be packed close to a layer of cells which is continuous with the upper cells of the radular sac, and which continually adds to their thickness by contributing more chitin. Here I ought to confess that my information on the subject of the chemistry of chitin is still rudimentary: to some extent I have been able to verify Zander's experiments,[1] which make it probable that chitin is a carbohydrate closely related to glycogen. If this were confirmed by chemical tests of some other kind, the result would be of great value to the student of chemical physiology in the mollusca. The chemistry of glycogen and its derivatives probably contains the secret of the snail's power of hibernation, and upon this, I think, depend the extraordinary modifications of the reproductive organs and processes with which we meet in this group.

Each uncus, as it leaves the matricial region, has a well-defined apex. This is that part which I have hitherto shown as the lower extremity of each 'tooth' in my drawings. For the reasons now apparent I shall treat it as the upper extremity. In many figures of radulæ it is omitted altogether.

The apex is usually provided with a furrow (*fossa apicalis*) into which the hinder part of the preceding uncus fits. It is further furnished in most cases with a vertical notch, a continuation upwards of the fossa.

The underside of the uncus is flattened and forms the *basal plate*; it becomes affixed to the *basal membrane*, or else is in some way, not yet well understood, imbedded in it. But the basal membrane shows no sign of being converted into chitin. I have applied Zander's tests for chitin to denuded pieces of basal membrane without result. Staining processes especially designed to act upon chitinous materials do not colour the basement membrane.

The hinderpart of the basal plate is generally somewhat wing-shaped, and it exhibits a line, more or less parallel to the transverse axis of the radula, approximately in the position which in a bird's wing is occupied by the outer edge of the primary coverts. Examination of isolated unci shows that this line is the edge, often thickened and adhering secondarily, of an actual fold: a relic of the original subconic configuration of the uncus. If one imagines a paper cone so folded that its margin is pointed in front and more or less squared at the back; two slits made in the sides of the cone, between front and back; the pointedness of the front margin increased by infolding along the sides of the slit, and a slight fold made on one or both sides of the squared part of the margin; the thickness of the point and other folded parts increased by dipping in melted paraffin,—a fair idea may be obtained thus of the building up of the uncus. To this fold on the basal plate I wish to give the descriptive term *lacinia*. It appears that in most cases the lacinia forms a kind of articulation with the fossa apicalis of the next uncus, so that the bases of the unci

[1] Pflüger's Arch. 66, 545 (1897).

Measurements.—Results of examination of selected typical specimens are here given in tabulated form. The numbers indicate micromillimetres.

	A.			B.			C.			D.			E.			F.			G.			H.			I.			K.		
Euparypha Pisana .	39	41	31	34	38	30	30	25	30	19	16	23	—	18	—	22	19	18	15	18	16	10	8	10	5	4	4	—	1	—
Cepæa hortensis . .	53	60	33	42	42	33	30	36	33	—	—	22	—	—	—	25	22	24	16	18	23	12	15	12	—	—	10	—	—	—
Cepæa nemoralis . .	60	62	52	42	48	30	28	34	41	—	—	32	—	—	—	30	32	26	24	26	25	10	12	12	—	—	7	—	—	—
Helicogena pomatia .	92	103	74	61	75	?	59	68	60	32	40	36	—	—	—	39	42	40	25	31	40	16	24	10	8	9	9	—	—	—
Helicogena aspersa .	60	69	40	44	56	28	36	43	40	20	30	28	—	36	—	34	35	27	27	34	25	16	14	16	6	10	10	—	8	—
Arianta arbustorum .	44	54	30	34	46	24	29	36	32	16	27	26	—	—	—	20	24	16	11	20	16	7	10	8	2	2	4	—	—	—
Helicigona lapicida .	31	30	12	21	21	10	14	13	20	—	—	—	—	—	—	18	20	18	18	18	18	9	10	9	—	—	6	—	—	—
Helicodonta obvoluta	26	28	10	19	20	8	16	19	13	[8	10]	10	—	[8]	—	12	14	12	8	10	12	7	6	6	4	2	2	—	—	—

Under each letter the first column gives the length in the case of the centrals, the second in the case of the admedians, the third in the case of the externals.

A = Length of basal plate.
B = From edge of lacinia to apex, in the middle line.
C = From apex to tip of mesocone.
D = From apex to tip of ectocone.
E = From apex to tip of endocone.
F = Width of basal plate across laciniæ.
G = Width of basal plate across ectoconic region.
H = Maximum width of mesocone.
I = Maximum width of ectocone.
K = Maximum width of endocone.

are dovetailed into one another. This is, however, not the case with the external unci of Helicids. In estimating the length of the basal plates this fact must be taken into consideration.

The basal membrane itself exhibits a *reticulum*, to be carefully distinguished from the outlines of the basal plates of the unci. This reticulum may be demonstrated by treatment with silver nitrate, or by staining with Kernschwarz.

In order to see the details of laciniæ and basal plates, and at the same time to avoid the production of an excessive number of false images, it is necessary to mount the radula in styrax.

Each radula (with few exceptions) presents us with unci of three different types, called central, admedian, and lateral; central, admedian, and marginal; or central, lateral, and marginal. (A few other variations of usage may be found.) The term transitional is also used to indicate unci intermediate in form between the second and third of these. To avoid confusion I shall call those unci of the second type, which lie nearest to the centrals, *admedians*; those of the third type I shall call *externals*. It will not be possible to mistake the application of these terms. When I wish to speak of admedian and external unci together I shall call them *pleuræ*, or *pleural elements*, the individual unci being *pleurals*. After careful examination I find I cannot recognize a special transitional type in the pleural unci. It is sometimes possible, in species like *H. lapicida*, to produce by staining the appearance of three vertical rows of unci in each pleura, but control experiments show that the number of vertical rows taking each combination of colouring matter depends upon the time of staining and the concentration of the stain used. The word transitional may, however, be still useful as an adjective to describe pleural unci intermediate between admedians and externals.

ADDITIONAL CHARACTERS.

[The first description in each case is that of the centrals, the second of the admedians, and the third of the externals.]

(*a*) Shape of basal plate.

Pisana. Wide, oblong; sides very little curved; rounded, upright, oblong.

hortensis. Long, narrow; long, narrow; upright, sub-quadrate.

nemoralis. Oblongate triangular, all sides curved; like wing of *Hesperia*; sub-tetragonal.

pomatia. Not regularly incurved except at sides, general shape of a square fitted to a triangle, both with rounded corners; sub-oblong, not markedly alate; very much like admedian, only slightly more quadrate.

aspersa. Truncated triangle, with sinuous sides; foot-shaped, heel displaced to side of hallux; oblong, nearly square.

arbustorum. Pointed oblong; bow-shaped; irregular tetragon.

lapicida. Double heart-shape; rounded truncated triangle; striated part a perfect rectangle.

obvoluta. Oblong, pointed, with convex sides; oblong, doubly angulated; oval.

(*b*) Character of lower corners of basal plate.

Pisana. Slightly curved; nearly straight; conterminous with lacinia, heavily striate.
hortensis. Long, with feathery striation; as central; slightly angular.
nemoralis. Slightly curved; slightly curved; with rounded corner.
pomatia. Rounded off; slightly projecting; nearly a right angle, sub-alate.
aspersa. Pointed, incurved; as central; very much thinned out.
arbustorum. Shape of *Vanessa* wing-tip; shape of *Platypteryx* wing-tip; distinct but blunt points.
lapicida. All small, but distinctly incurved.
obvoluta. Pointed, slightly incurved; sharply incurved; rectangular, erect.

(*c*) Shape of lower edge of basal plate.

Pisana. Nearly straight; straight; scarcely sinuated.
hortensis. Indented, angle 130°; crenulated, sharply descending towards central; straight, internally curved.
nemoralis. Roughly straight, with large indentation; double curve, out and in; irregular.
pomatia. Nearly straight, no indentation; very slightly concave, descending towards central; straight, inclined towards central.
aspersa. Two semicircles side by side; outside a semicircle, inner half a slanting line; irregular.
arbustorum. Fringed; fringed; irregular.
lapicida. Bracket-shaped; slightly curved, inner half crenulated; irregularly convex.
obvoluta. All straight.

(*d*) Shape of apex.

Pisana. Rounded, flattened; as central; roughly squared, central indent and external notch.
hortensis. Bifid, rounded; entire, rounded, but tendency to point on inner side; nearly straight, with two lateral indentations.
nemoralis. Trifid; rounded; irregularly convex.
pomatia. Almost straight, slightly irregular sinuations; as central, but inner third curving downwards; as admedian.
aspersa. Very convex, with additional central convexity; as central; straighter, but with central protuberance.
arbustorum. Like end of a hexagon, but centrally split; rounded; long and pointed.
lapicida. Convex, with central notch; an obtuse angle; bifid, hardly produced.
obvoluta. Nearly straight, with central notch; nearly straight; convex, projecting.

(*e*) Lacinia parallel with lower edge of basal plate or otherwise.
(*No entry means that the lacinia is parallel.*)

Pisana. External almost coincident.
hortensis. External almost parallel with outer side of basal plate.
nemoralis. As *hortensis.*
aspersa. Admedian lacinia angulate; external irregular.
arbustorum. Central and admedian not parallel (diagonal).
lapicida. Conspicuously at right angles to central axis, not following the curves of the margin.
obvoluta. Central and admedian diagonal; external coincident.

(*f*) Number and character of cones visible.

Pisana. 3; 3; 2 (mesocone bifid).
hortensis. Rounded tongue-shaped point, narrower base; as central, but more quadrate base; 2 (mesocone bifid).
nemoralis. 1, blunt, thick, angular at summit; as central; 2 (bifid mesocone and conical ectocone; sometimes additional ectocones).
pomatia. 3; 2; 2 (bifid mesocone, but not rarely found entire).
aspersa. 3 (mesocone ovate and overlapping others); 3 or 2 (endocone only apparent, really part of mesocone); 2 (mesocone bifid; ectocone rarely duplicated).
arbustorum. 3 (long pointed mesocone, small curling ectocones); 2 (as central); 2 (mesocone bifid; sharp, especially ectocone).
lapicida. 1; 1; 2, but ectocones frequently duplicated.
obvoluta. 1 (slight notches representing side cones); 1 (a slight notch representing ectocone); 2 (claw-like bifid mesocone).

It is hoped that the above additional characters may serve for the differentiation of the species in detail; they are therefore tabulated under characters, and not primarily under species. In comparing such minor points allowance must be made for individual variation.

It remains to summarize what appear at present to be the points of diagnostic value; the tables will be found to contain much more, if further confirmation be needed in any case.

Helicogena pomatia is remarkable for showing very little diminution of size in the external unci. The radula is very broad in comparison with that of *aspersa.* The endocones of the external unci are so little prominent as to be hardly noticeable at first sight.

Helicogena aspersa is characterized by the presence of distinct, though small, accessory cones.

Euparypha Pisana has these cones very distinct, otherwise being planned very much on the same lines as *Helicogena.*

The *Cepææ* have the accessory cones absent or obsolescent in mature specimens: *nemoralis* has normally a trifid apex, *hortensis* a bifid one. The basal plates of *hortensis* are much longer in proportion than those of *nemoralis.*

Arianta is marked by the exceptional length of the cones, and yet more clearly by the arcuate shape of the basal plates.

Helicigona cannot well be confounded with those just named. The cones in all regions are very obviously rounded, and the basal plates partake of the same character.

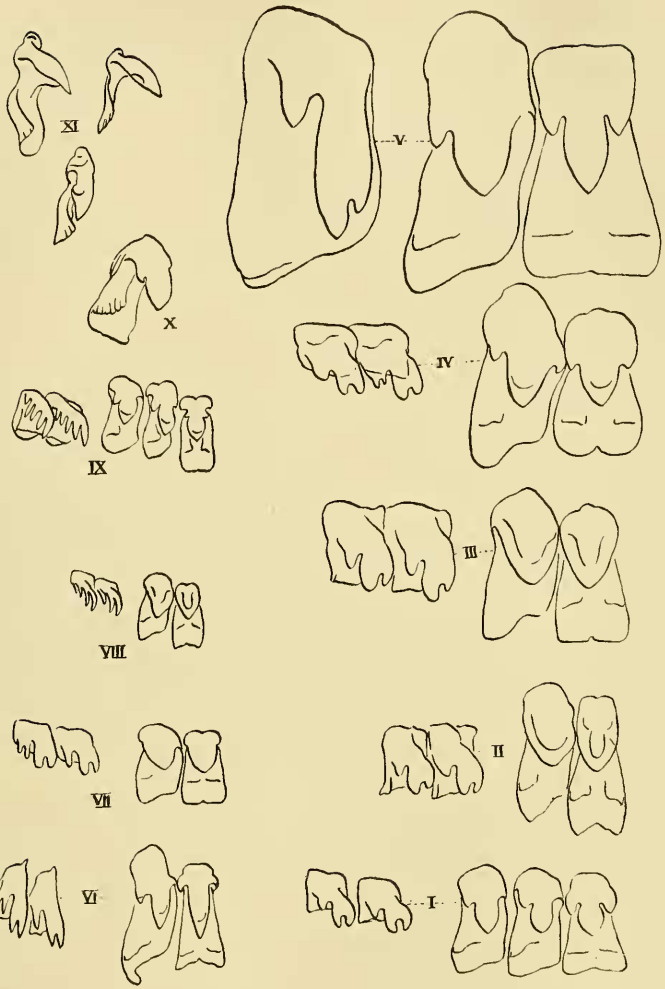

Fig.

I. Typical unci from the radula of *Euparypha Pisana* (Müll.).
II. ,, ,, ,, *Cepæa hortensis* (Müll.).
III. ,, ,, ,, *Cepæa nemoralis* (Müll.).
IV. ,, ,, ,, *Helicogena aspersa* (Müll.).
V. ,, ,, ,, *Helicogena pomatia* (L.).
VI. ,, ,, ,, *Arianta arbustorum* (L.).
VII. ,, ,, ,, *Helicigona lapicida* (L.).
VIII. ,, ,, ,, *Helicodonta obvoluta* (Müll.).
IX–XI, see text, *ad fin.*

Helicodonta may be recognized by the claw-like externals. The long oval shape of the central basal plate is also unmistakable.

On the preceding page figures are given of the species above described. The scale employed is the same throughout; the size of the individual parts may be ascertained by reference to the table on p. 207.

Figs. X and XI are from specimens showing the extreme ends of the radula, stained with carbol fuchsin. They will serve to illustrate what has been said about the lacinia.

Fig. IX is from a young example of *C. hortensis*, and illustrates the point that the accessory cones are always more distinct and visible in the younger examples. At a still earlier stage the radula may be said to be Endodontid in type.